I. LEAF ANATOMY.

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(Twenty-five Text-figures.)

[Read 24th June, 1959.]

Synopsis.

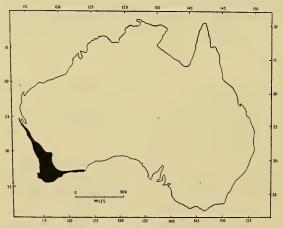
Anatomical features of the leaves of selected species of *Conostylis* are described and illustrated and their systematic and ecological significance discussed briefly.

INTRODUCTION.

Occurrence and Habit.

The genus *Conostylis* is restricted to a small area in south-western Australia where it is a conspicuous member of the Liliiflorae in all but the wettest vegetation communities.

In habit, there is extreme diversity between the different species. All are perennials and many have a strong capacity for vegetative reproduction which may be by means of stolons, rhizomes or a method of growth referred to by Bentham (1873) as proliferous branching. The habit may therefore be prostrate and spreading, caespitose



Text-fig. 1.—Distribution of the genus Conostylis. The occurrence within this area of the species dealt with in the present paper is indicated in Table 2.

or almost shrubby, some plants attaining a height of 50-60 cm. There is nearly always a large amount of sclerenchyma in the leaves, stems and roots, and a number of species bear harsh spines on the leaf margins. The flowers and flowering scapes of practically all species bear a dense, woolly tomentum of branched trichomes.

Materials and Methods.

The data presented have been derived from foliar cross sections prepared largely from fresh material fixed in the field, although some species have, of necessity, been studied from herbarium material; in the latter case leaves were boiled in water for a few minutes before being sectioned. Measurements on specimens, part of the leaves of which were fixed fresh, while the remainder was thoroughly pressed and dried, showed that the maximum shrinkage likely in dried herbarium material was of the order of 10% (linear measurement) compared with fresh specimens. On boiling for a few minutes the original size was restored.

Difficulties were encountered in attempts to microtome this material, probably due to the extremely fibrous nature of the leaves of most species. Satisfactory hand sections were obtained and were stained with safranin and fast green (Johansen, 1940) and made permanent.

Camera lucida drawings were employed throughout.

GENERAL STRUCTURE.

The chief feature of taxonomic importance is the disposition of sclerenchymatous tissue in the vicinity of the vascular bundles. By considering, in addition, lignification of the epidermal cell walls, presence or absence of tannin-containing cells, occurrence of large subepidermal cavities, leaf shape and the occurrence of surface hairs and protuberances, it has been possible to identify the twelve species dealt with here.

A developmental feature of interest lies in the origin of the two surfaces of the lamina. Although exhibiting, in cross section, a structure similar to that of an isobilateral leaf, such as is found in species of *Eremophila* or *Eucalyptus*, the disposition of the conducting tissues in the mature leaf of *Conostylis* has resulted from the ontological fusion of the two halves of the plicate sheathing base (Text-fig. 24). By this process the adaxial surface has been highly reduced and the two lateral surfaces of the mature part of the leaf are each abaxial. Arber (1925) has described this phenomenon in *Romulea, Galaxia* and some other monocotyledonous genera.

Because almost the entire leaf surface is abaxial, some difficulty arises in describing the orientation of structures within the leaves. For the purpose of this study the terms upper or lower are abandoned in referring to the leaf surfaces; instead, structures in the vicinity of either epidermis will be referred to as *outer*, while by the *inner* part of the leaf will be meant the region near the imaginary line of fusion of the two halves of the lamina.

HISTOLOGY.

Epidermis.

Typical cells are more or less isodiametric, having a diameter of $20-30\mu$; the largest observed were about 80μ in diameter. The cell walls are commonly heavily lignified and are often tangentially compressed (Text-fig. 12), but sometimes are thin and parenchymatous.

The thickening material appears to be lignocellulose, said to be a "relatively infrequent component of epidermal walls" (Linsbauer, quoted by Esau, 1953). Several species show stratification in the walls (Text-fig. 14). Pit pairs are frequently seen, particularly on the inner tangential and the radial walls. The cuticle is commonly $1-2\mu$ thick. Stomata are usually neither deeply sunken nor exserted; exceptions are mentioned specifically below.

The determination of stomatal frequency from the examination of leaf-reconstructions from cross sections might prove easier than from surface counts which, in this genus, are hampered by the presence of hairs and ridges on the leaf surface in some species. Measurements of stomatal frequency and size of guard cells are of interest in the case of *C. setigera*, which is thought to be a polyploid derivative of *C. setosa* (Green, 1958).

Multicellular trichomes arise from the laminar epidermis of some species, while in others marginal spines or setae consist of fibrous outgrowths of the epidermis. The leaf blade trichomes are of the branched candelabra type (Esau, 1953) (Text-fig. 2), while the marginal spines or setae may be minutely branched on the upper side or entire.

Palisade.

In the present paper the term *palisade* is used to denote the principal (and usually palisade-like) photosynthetic tissue of the mesophyll. The term *storage parenchyma*

All works and the second se					mining T and the	Other I confitted	Cuticle	Toridomol	Palisad	Palisade Cells.	Storage
				Rumber Examined.	Typical Locality.	Outer Localities.	1111CKUESS. (µ)	Cells.	Radial.	Tangential.	Farencnyma Cells.
1. C. stylidioides	:	:		63	North of Geraldton.	East of Geraldton.	I	15	30	12	45
3. C. candicans	:	:	:	4	Nedlands.	Rottnest Island.	I	15-20	30	15	35
4. C. setosa	:	:	:	61	National Park.	Kalamunda.	1	10	40	10	40-50
5. C. androstemma	:	:	:	e	Kalamunda.		1 · 7	45×15	45	15	02
6. C. petrophiloides	:	:	:	1	Newdegate.		2.5	80×20	30	10	40-80
7. C. vaginata	:	:	:	61	North of Hopetoun.	Near Hopetoun.	4	30×15	50	15	20-80
8. C. setigera	:	:	:	4	King's Park.	Medina.	$1 \cdot 2$	14	38	12	45
9. C. juncea	:	:	:	3	Bassendean.	Applecross.	2.3	15-20	34-45	15	30-60
10. C. bealiana	:	:	:	67	Esperance.		2	20	30	10	30-100
11. C. caricina	:	:	:	4	Near Toodyay.		2.3	60×30	50	10	20-80
12. C. aculeata	:	:	:	11	East of Geraldton.	North of Geraldton, Darling Range, South-west.	ŝ	10	30	12	20-30
• All dimensions are of average cell diametric in transverse section the radial	are of a e sectio	average n the	e cell d radial	liameters in μ . and tangential	liameters in μ . For cells showing considerable variat and tangential diameters are joined by the sign \times .	diameters in μ . For cells showing considerable variation from the mean the extreme range is shown; for cells which are markedly aniso- t and tangential diameters are joined by the sign \times .	the extreme	range is shown	a; for cells	which are ma	rkedly aniso-

TABLE 1.*

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THE GENUS CONOSTYLIS. I,

is used to refer to the remaining tissue of the mesophyll, exclusive of the vascular tissue. It may or may not contain chloroplasts and is only rarely spongy.

The palisade consists typically of 2 layers of cells about $15 \times 7\mu$, occurring directly beneath the epidermis on both sides of the leaf. It may be in the form of a continuous band around the leaf or it may be interrupted by girder-like masses of sclerenchyma surrounding the vascular bundles and extending on the outside to the epidermis. In *C. aculeata*, whose leaves are characteristically of the interrupted type in the mature state, inspection of soft vigorous regrowth following a fire revealed an uninterrupted palisade.

In one species, C. *juncea*, large subepidermal parenchymatous cells have been observed within the palisade. These cells are ovoid in both cross section and longitudinal section, are much larger than the palisade cells, and have occurred regularly in all leaves examined (Text-fig. 18).

The cells of the palisade are thin-walled and the tissue may either be sharply demarcated from or merge indistinctly into the storage parenchyma.

Storage Parenchyma.

The storage cells are usually more or less isodiametric with slightly thickened walls and the intercellular spaces inconspicuous. Sometimes the storage parenchyma appears spongy with small, regular intercellular spaces (Text-fig. 18).

Chloroplasts are found usually in diminished numbers toward the inside of the leaf, but rarely are almost as dense as in the palisade (Text-fig. 4). Cells with darklystaining contents, presumably phlobaphene, an oxidation product of tannins (Johansen, 1940), occur prominently in the storage parenchyma and sometimes in the palisade (Text-fig. 20 and 25). These cells appear pale to dark brown in unstained sections and almost black with safranin and fast green; their presence appears characteristic of five species (Table 2).

Vascular Tissue.

Almost without exception, the most striking feature of the vascular bundles is the occurrence of large areas of sclerenchyma associated with the conducting tissues. In many cases the conducting elements are completely surrounded by a *mestom* sheath (Schwendener, quoted by Esau, 1953); sometimes the fibres immediately adjacent to the phloem have a distinctive appearance (smaller lumen and differential stainability).

Often the mestom sheath is in turn surrounded by a prominent parenchymatous sheath which may be entire or broken where the phloem fibres extend outward to join the epidermis (Text-fig. 6 and 12 resp.).

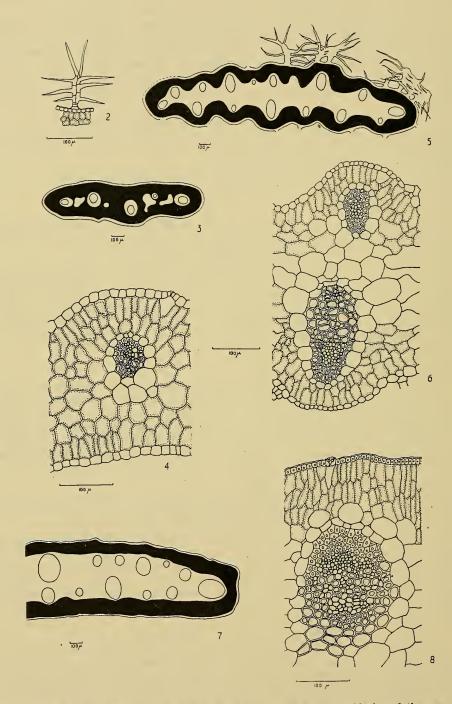
The cells of the xylem and phloem call for no special comment. Phloem has been observed clearly in sections cut from herbarium specimens more than fifty years old, its preservation evidently being due to the protection of the fibrous sheath.

The vascular bundles occur in two rows in the flat leaves, often with larger and smaller bundles alternating (Text-fig. 5). As a result of the developmental fusion of the sheathing leaf base, the bundles are oriented with the phloem toward the outside. In one species, *C. aculeata*, the larger bundles are united in pairs in the girder-like mass of sclerenchyma (Text-fig. 25), while in another, *C. setigera*, three bundles are commonly united within a mass of sclerenchyma which does not reach the epidermis (Text-fig. 16).

SPECIFIC ANATOMICAL DESCRIPTIONS.

In the following descriptions," twelve species have been chosen as being representative of the main types of anatomical structure observed in the genus. The names of other species whose anatomy is essentially similar are appended to each description. The arrangement is approximately in order of increasing degrees of xeromorphism, as inferred from the disposition of the sclerenchyma, presence of tannin cells, leaf tomentum and form and other minor characters (Table 1).

The descriptions are based on single preparations, chosen as typical of the species as a result of the examination of leaves from as many localities as possible. In most



Text-fig. 2-8.—In the low-power diagrams the palisade is shown in black and the vascular bundles in outline. 2, C. candicans, a small but otherwise typical example of a candelabra-type trichome; 3-4, C. stylidioides; 5-6, C. candicans; 7-8, C. setosa.

cases leaves from 3 or 4 localities throughout the range were examined in conjunction with the particular leaf described below, but in some cases only one specimen was available; the details are set out in Table 1. The dimensions of component cells found to be most variable are shown, with measurements from a typical preparation.

1. CONOSTYLIS STYLIDIOIDES F. Muell. (Text-fig. 3-4.)

This species is almost alone in the genus in its paucity of the xeromorphic characters so common in most other species, although a loose tomentum can occur on the leaf surface in plants from some parts of the range (notably to the west of Geraldton). The remarkable absence of lignification is reflected in the flaccid nature of the leaves.

Epidermal cells are thin-walled and isodiametric; the stomata, if anything, are slightly exserted. The palisade merges indistinctly into the storage parenchyma. The number of chloroplasts in the storage parenchyma is scarcely less than in the palisade, except for an ill-defined zone of central cells which contain no chloroplasts. The vascular bundles are scarcely strengthened, the inner sclerenchymatous sheath being reduced to very few (5-8) fibres in most cases. The cells of the parenchymatous sheath are slightly more regular than those of the storage parenchyma and contain no chloroplasts. *C. prolifera* Benth., *C. racemosa* Benth.

2. CONOSTYLIS SEORSIFLORA F. Muell.

Similar to the above, except for the presence, in the single specimen examined, of lignified walls in the epidermal cells immediately adjacent to the vascular bundles. The remainder of the epidermis is parenchymatous.

3. CONOSTYLIS CANDICANS Endl. (Text-fig. 5-6.)

A prominent anatomical feature of the leaves is the presence of large, multicellular, branched trichomes arising from the epidermis. These give the leaf its characteristic mealy appearance in surface view.

Epidermal cell walls are unlignified and the cells are more or less isodiametric; from the epidermis arise numerous candelabra-type trichomes similar to those occurring on the scape and perianth of most species (Text-fig. 2). These consist of a central axis of 4 longitudinal series of cells; the lower 1-2 layers bear no projections, but the 3-4 above bear aciculate protuberances in each of 4 directions, approximately at right angles to the axis. The phloem is capped by 3-4 layers of fibres which occasionally become produced outward to the epidermis, interruping the palisade. A parenchymatous outer sheath occurs prominently. C. dealbata Lindl.

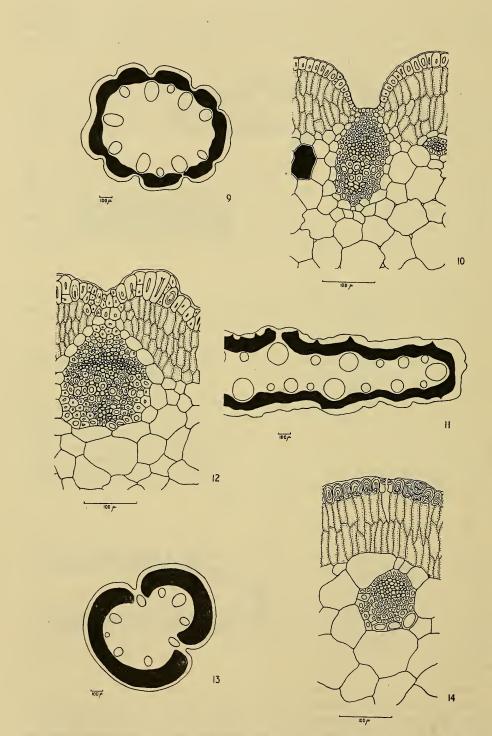
4. CONOSTYLIS SETOSA Lindl. (Text-fig. 7-8.)

No single outstanding feature characterizes this species. The leaf is more rectangular in section than in other species, the palisade is uninterrupted and pairs of bundles occasionally may be more or less united by the fusion of their fibrous sheaths on the inside.

The epidermis consists of isodiametric cells having lignified walls and a small lumen. The palisade is continuous and clearly demarcated from the storage parenchyma whose cells may be more or less spongy, with very few chloroplasts. The vascular bundles are each surrounded by a fibrous sheath, in turn surrounded by a parenchymatous sheath, except in the rare cases when the fibrous sheaths of two opposite bundles coalesce.

5. CONOSTYLIS ANDROSTEMMA (Lindl.) F. Muell. (Text-fig. 9-10.)

Leaves of this species are more or less circular in section with deep, longitudinal grooves. By comparing Text-figures 9 and 21 it may be seen that such grooves may occur opposite (i.e., on the same radius) or between the major bundles, in different species. Further observations will be necessary to confirm the taxonomic value of this character, which appears uniform in the species examined. The sole exception



Text-fig. 9-14.—9-10, C. androstemma; 11-12, C. petrophiloides; 13-14, C. vaginata.

occurs in an undescribed subspecies of *C. androstemma*, geographically removed from the typical subspecies here described and illustrated, in which the grooves of the single specimen examined were between the major bundles. Tannin cells occur in the storage parenchyma.

Epidermal cells are anisodiametric, with walls heavily lignified. In some places the space normally occupied by one epidermal cell is occupied by two or three, one above the other. This condition will be referred to by the term *multiple epidermal cells*; in no way does it refer to a hypodermal layer, being restricted to the occurrence of multiple cells in an otherwise single-layered tissue (Text-fig. 10, 12, 14, 18, etc.). The palisade tissue merges into the storage parenchyma whose cells do not appear spongy in spite of small regular intercellular spaces. Many storage cells adjacent to the palisade may contain deposits of tannin; one section showed 11 tannin-containing cells in the outer storage parenchyma. The usual fibrous and parenchymatous sheaths surround the bundles, the latter less prominently than in many other species. The fibrous sheath of the larger, alternate bundles often penetrates the palisade to join the epidermis.

6. CONOSTYLIS PETROPHILOIDES F. Muell. ex Benth. (Text-fig. 11-12.)

A particularly heavily lignified epidermis occurs in this species. Striations, multiple cells and pits are characteristic. The palisade is practically continuous.

The epidermal cells are markedly anisodiametric, being greatly compressed tangentially. The cell walls are lignified, striated and pitted and the cells contain, as a rule, a small compressed lumen. Multiple cells are very common. Stomata are slightly exserted. The palisade lies in a practically continuous band and is clearly demarcated from the adjoining tissues. The storage parenchyma cells do not appear spongy and do not contain chloroplasts. The conducting tissues are immediately surrounded by several layers of fibres, in turn surrounded by a parenchymatous sheath which is rarely broken.

7. CONOSTYLIS VAGINATA Endl. (Text-fig. 13-14.)

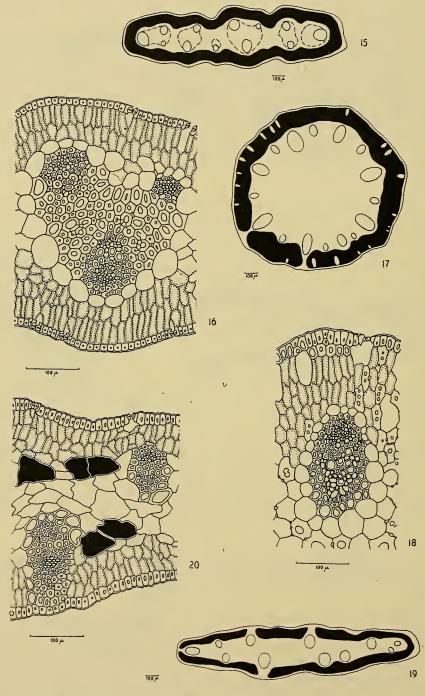
The leaves are more or less circular in section and the palisade is often in a continuous band. When the palisade is interrupted, the epidermis is deeply grooved at the point of interruption (Text-fig. 13). Epidermal cell walls are heavily lignified, striate and pitted, and multiple cells occur infrequently.

Epidermal cells are anisodiametric with occasional multiple cells. The walls are heavily lignified, with prominent striations and pits on the inner tangential and radial . walls. The palisade forms a very regular band, sharply distinct from the storage parenchyma which contains no chloroplasts. The vascular bundles are each surrounded by a fibrous and a parenchymatous sheath, the latter not well defined and occasionally broken by the fibrous sheath when it is produced outward to the epidermis.

8. CONOSTYLIS SETIGERA R.Br. (Text-fig. 15-16.)

A large area of fibres often encloses three vascular bundles and the palisade is always continuous. These features produce an appearance in this species (and its relatives, C. melanopogon and C. psyllium) quite unlike that in any other species in the genus.

Epidermal cells are small and isodiametric with the walls heavily lignified. The palisade is regular and continuous and the storage parenchyma, small in extent, contains chloroplasts. Each fibrous bundle sheath encloses, typically, three vascular bundles; the sheath is usually one cell thick on the outside of the bundles, but the whole of the more or less triangular region within the three bundles consists of a mass of fibres. Pit pairs occur in the walls of many of these cells. The individual bundles are smaller than in many other species. A prominent parenchymatous sheath surrounds each group of three bundles and its fibrous matrix. C. melanopogon Endl., C. psyllium Endl.



Text-fig. 15-20.-15-16, C. setigera; 17-18, C. juncea; 19-20, C. bealiana.

9. CONOSTYLIS JUNCEA Endl. (Text-fig. 17-18.)

This species is distinguished by the presence of large subepidermal cells bearing a superficial resemblance to substomatal chambers. The storage parenchyma cells have intercellular spaces which give this tissue an appearance unlike that of any other species examined.

Epidermal cells are anisodiametric with occasional multiple cells, and the coll walls are heavily lignified. The palisade contains prominent subepidermal cells which are ovoid in both transverse and longitudinal section; however, the reliability of this as a taxonomic character cannot be estimated until the exact nature and constancy of the cells is known. They occur irregularly around the leaf, 20 being counted in one typical section. The palisade for the most part is continuous, but is usually interrupted at one or two places by the outward extension of the fibrous bundle sheath; it merges into the storage parenchyma, the cells of which resemble somewhat the typical spongy mesophyll found in the leaves of many genera, e.g., *Lilium*. Small regular intercellular spaces may be seen both in section and surface view of the cell walls. The vascular bundles are each surrounded by a fibrous sheath which may protrude through the outer, enclosing parenchymatous sheath, to join the epidermis.

C. involucrata Endl.—Note: Flat-leaved forms of C. juncea, placed under C. involucrata by Bentham (1873), cannot be maintained as a separate species, since terete and flat leaves occur frequently on a single plant. The anatomical structure of the flat leaves retains the spongy parenchyma and the subepidermal cells described above, although the general pattern resembles a flat-leaf type such as C. bealiana (Text-fig. 19-20).

10. CONOSTYLIS BEALIANA F. Muell. (Text-fig. 19-20.)

Many prominent tannin-containing cells occur in the storage parenchyma of the leaves of this species. The palisade is well defined and interrupted by many of the fibrous bundle sheaths which extend to the epidermis.

Epidermal cells are isodiametric with heavily lignified walls. The palisade consists typically of 2 cell layers which are sharply distinct from the storage parenchyma. The storage cells contain no chloroplasts; they are irregular in shape in the only specimens examined, but there is no reason to believe that this is due to distortion arising from the preparation of the herbarium specimens used, since this appearance was not seen in other species where comparison between living and herbarium material was possible. The outermost cells of the storage parenchyma are frequently very large and contain tannin-like deposits; no chloroplasts occur in this tissue. The vascular bundles are surrounded by a fibrous sheath which often penetrates the surrounding parenchymatous sheath to join the epidermis.

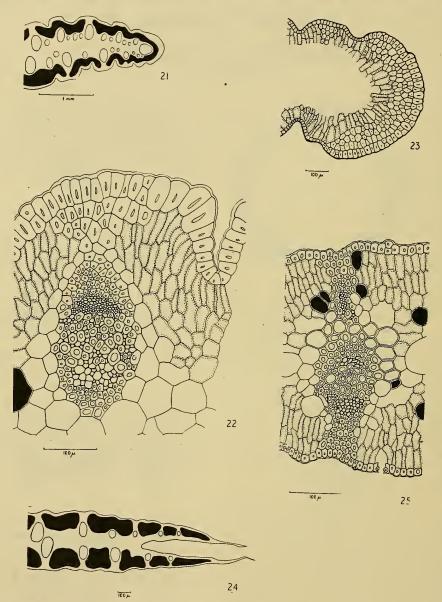
11. CONOSTYLIS CARICINA Lindl. (Text-fig. 21-22.)

The leaves are characterized by their large cross sectional area, the presence of tannin cells in the storage parenchyma and an extremely heavily thickened epidermis.

Epidermal cells are tangentially compressed, larger than in all other species, with heavily lignified walls; multiple cells occur infrequently. Stomata are confined to grooves in the epidermis. The palisade is deeper and consists of more layers of cells than in the other species; it occurs in a well-defined layer merging into the storage parenchyma. Tannin cells occur infrequently in the outer cell layers of the storage parenchyma. The vascular bundles are each surrounded by a fibrous sheath which, in many bundles, penetrates the parenchymatous sheath, interrupting the palisade, to join the epidermis.

12. CONOSTYLIS ACULEATA R.Br. (Text-fig. 23-25.)

The most prominent feature of the leaves of this species is the occurrence of girderlike masses of sclerenchyma, across the whole width of the section, from epidermis to epidermis, enclosing usually two vascular bundles. Several layers of heavily lignified hypodermal fibres occur at the margins. Epidermal cells are isodiametric with heavily lignified walls; the epidermis is trequently undulate with grooves occurring between the vascular girders (see discussion under *C. androstemma*) or the epidermis may be more or less flat. At the margins



Text-fig. 21-25.—21-22, C. caricina; 23, Hypodermal fibres in a form of C. aculeata; 24-25, C. aculeata, the low power diagram showing the plicate sheath near the base of the leaf.

occur several to many layers of hypodermal fibres (Text-fig. 23). It is upon this last character that the species *C. bromelioides* is based; in this species the thickening is sufficiently heavy to be conspicuous exomorphically. The palisade is much dissected by the vascular girders; it merges into the storage parenchyma, cells of which contain chloroplasts and frequently tannin. The parenchymatous bundle sheath is reduced to a single layer of cells on each side of the fibrous girder. The girder structure is developed most strongly in certain related species such as *C. robusta* and *C. bracteata*; in all cases it represents the coalescence of two fibrous bundle sheaths when the bundles are heavily strengthened and occur directly opposite one another. C. breviscapa R.Br., C. bracteata Lindl., C. bromelioides Endl., C. preissii Endl., C. harperiana W. V. Fitzg., C. teretiuscula F. Muell., C. spinuligera F. Muell. ex Benth., C. serrulata R.Br., C. laxiflora Benth., C. cymosa F. Muell. ex Benth., C. phathyrantha Diels.

DISCUSSION.

Ecology and Geographical Distribution.

Attempts to correlate anatomical features of the leaves of *Conostylis* species with geographical and ecological ranges have proved disappointing. Table 2 shows that when the species are arranged according to the degree of development of xeromorphic characters the leaf anatomy does not reflect the influence of the present environment. Of the two species which never occur on sand (*C. setosa* and *C. caricina*) no characters

					LABLE 2.					
		Epidermal Cell Walls Lignified.	Palisade Interrupted,	Bundles United.	Tannin Cells Present.	Terete Leaves.	Laminar Trichomes,	Soil Types.*	Distribution.†	Annual Average Rainfall (cm.).
1. C. stylidioides		_	_	_	_	_	-	S-C	CW-NW	25-50
2. C. seorsiflora		±	_	-		-	·	s	S-SE	50 - 75
3. C. candicans			-		_	-	+++	S–C	CW-NW	25 - 100
4. C. setosa		+	-	_	_	-	-	С	CW	100
5. C. androstemma		+	±	- '	+	+	-	s	CW	37
6. C. petrophiloides		+	· ±		-	-	-	S	C-SE	25 - 50
7. C. vaginata		+++	±		-	+	-	s	S-SE	45-50
8. C. setigera		+	-	+++	—	-	-	S-C	S-SW-CW	75-100
9. C. juncea		++	±	-	±	±	-	s	CW	75-100
10. C. bealiana		+	++		+++	-	-	S	SE	50-75
11. C. caricina		+++	+		++	-	— .	С	CW	100-110
12. C. aculeata	••	++	+++	++	+	-	-	S-C	NW-CW-	30-125
									SW-S	

TABLE 2.

* S=sand, siliceous or calcareous; C=clay, including lateritic soils.

† Refers to the following broad areas in the South-West Vegetation Province: C=central, NW=north-west, CW=central-west, SW=south-west, S=south, SE=south-east.

of the foliar anatomy separate them from other groups of species. Of the remaining species examined the following grow commonly in sandy situations, but have been recorded also in clayey soils: *C. stylidioides, C. candicans, C. setigera* and *C. aculeata*; once again, no anatomical character or group of characters separates these out as a group. The same situation exists with regard to geographical distribution and rainfall. Anatomical characters are therefore genetically controlled and are not modified to any great extent by the environment.

Systematics.

In many cases anatomical characters have proved closely correlated with those determining systematic affinity. This is to be expected, since the exomorphic characters employed in determining species boundaries frequently reflect some internal anatomical feature. The following groups of species, shown as being anatomically related in the foregoing descriptions, are recognized by Bentham (1873) as being closely related on exomorphic characters:

- 1. C. stylidioides, C. prolifera, C. racemosa.
- 2. C. candicans, C. dealbata.
- 3. C. setigera, C. melanopogon, C. psyllium.
- 4. C. juncea, C. involucrata.
- 5. C. aculeata, C. bracteata, C. bromelioides, C. preissii, C. spinuligera, C. serrulata, C. laxiflora, C. cymosa.

Key to the Species examined, based on Anatomical Characters.

1. Palisade continuous. 2.* Vascular bundles discrete. 3. Epidermal cell walls thickened and lignified. 4. Leaves terete. 5. Tannin cells occurring in the mesophyll. 6. Epidermis ± smooth; prominent subepidermal cells in the palisade 6.* Epidermis undulate; subepidermal cells absent 5. C. androstemma. 5.* Tannin cells absent 7. C. vaginata. 4.* Leaves flat. 7. Prominent subepidermal cells in the palisade; leaves often \pm terete ... 9. C. juncea. 7.* Palisade of chlorenchyma cells only. 8. Margins notably square in section; subepidermal fibres absent 4. C. setosa. 8.* Margins rounded; prominent rows of subepidermal fibres 6. C. petrophiloides. 3.* Epidermal cell walls thin and mostly parenchymatous. 9. Epidermal cells adjacent to vascular bundles lignified, otherwise parenchymatous 2. C. seorsiflora. 9.* Epidermal cells entirely parenchymatous. 10. Epidermis bearing a heavy grey tomentum of branched trichomes 10.* Trichomes sparse or absent on leaf surface 1. C. stylidioides. 1.* Palisade interrupted by an extension of the fibrous bundle sheaths, commonly of alternate bundles. 11. Alternate pairs of vascular bundles united in a sclerenchymatous girder passing across the section from epidermis to epidermis 12. C. aculeata. 11.* Vascular bundles discrete. 12. Leaves terete. 13. Epidermis smooth; prominent subepidermal cells in the palisade 9. C. juncea. 13.* Epidermis undulate or grooved. 14. Epidermis with grooves adjacent to alternate vascular bundles 14.* Epidermis with one or two grooves only, adjacent to fibrous interruptions of palisade 7. C. vaginata. 12.* Leaves flat. 15. Tannin cells occurring in the mesophyll. 16. Epidermal cells ± isodiametric; palisade of 2 cell layers 10. C. bealiana. 16.* Epidermal cells tangentially compressed; epidermis of 3 cell layers 11. C. caricina. 15.* Tannin cells absent. 17. Prominent subepidermal cells in the palisade 9. C. juncea. 17.* Palisade of chlorenchyma cells only 6. C. petrophiloides. Acknowledgements.

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